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Conserving migration in a changing climate, a case study: The Eurasian spoonbill, *Platalea leucorodia leucorodia*

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ABSTRACT

Migratory species are fundamental for the long-term maintenance of biodiversity, as well as for the ecological functions they provide. Their current protection, however, lacks a clear understanding of how conservation areas are able to maintain the connectivity of populations in different periods of the migration cycle. Such a problem is even more significant in light of the consequences of climate change on the availability of suitable habitats, especially for those species for which the effects can be amplified by the long distances covered during migration. Here, a graph-theoretic approach was implemented to test for the relationship between current and projected climate conditions on the connectivity of conservation areas for migratory birds. The framework was tested by considering the migration system of the northwestern populations of Eurasian spoonbill (*Platalea leucorodia leucorodia*), characterized by mid-long-range movements between the breeding sites in the Netherlands and wintering sites in Spain, Senegal and Mauritania. Climate effects suggest an ever-increasing range of distances to cover by the spoonbills, increasing the separation between important stopover and wintering areas. The current spatial configuration of areas will hardly support the long-range spoonbill migration, increasing the risk of fragmentation and contraction of populations, unlikely to support the spoonbill migration system. The methodology described can be applied to other migration systems, incorporating useful information in the implementation of conservation policies able to identify important areas for the long-term persistence of biodiversity.

1. Introduction

Animal migration is probably one of the most fascinating and complex phenomena in nature, occurring as adaptive response to the seasonal and geographic variation of resources (Gauthreaux Jr, 1982). Examples are the regular movement of birds between breeding and wintering sites (Dingle and Drake, 2007), altitudinal displacements in bats (McGuire and Boyle, 2013), or the vertical movements of copepods through the water column of oceans (Darnis and Fortier, 2014). Migrations can be also a source of important ecosystem services, such as the redistribution of nutrients by the grazing activity of wildebeest in the Serengeti (Holdo et al., 2011), or the control of insect populations by the feeding activity of migratory birds (Wilcove and Wikelski, 2008). Given the peculiarity of this phenomenon, which involves a large number of individuals in space and time, migratory species are more susceptible than non-migratory ones to a series of specific threats (e.g. habitat loss/fragmentation, overexploitation, climate change), able to hinder the persistence of populations (Sanderson et al., 2006; Mantyka-Pringle et al., 2012).

Among many, climate is one of the most important factors in determining changes in the distribution and geographical range of birds, influencing their migratory activity through the alteration of *en route* conditions (e.g. conditions at stopover sites) and their phenological and/or behavioural responses (e.g. time of migration) (Strode, 2003; Pulido and Berthold, 2004; Parmesan, 2006). Specific life-history traits, such as the migratory behaviour (e.g. obligate, partial, long and short migration strategies) allow constraining the phenological response to rapid climatic changes in avian species (Rubolini et al., 2010). Short-distance migrants could benefit from changing climate conditions because of an earlier start to the reproductive season, meaning longer seasons and opportunity for more offspring (Lehikoinen and Sparks, 2010). On the other hand, long-distance migrants may not benefit from such changes, since the beginning of the reproductive cycle is dictated by the spring arrival date (Both et al., 2010). For example, birds in the Palearctic-African migration system are likely to be constrained by the onset of the dry season in the Sahara rather than by the conditions of the breeding grounds, being forced to move before the Sahara's dry season to allow a more successful migration (Jenni and Kéry, 2003). Therefore, besides the endogenous rhythms controlling the migratory activity, the availability of suitable habitats and food resources during

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Table 1
Brief overview of the most common terms used in this work.

Node	The fundamental unit of which graphs are formed. In this work, nodes correspond to conservation areas or sites.
Graph (or network)	The graphical representation of the relationship between nodes. In this work, it represents the pattern of species movement.
Link	Connection between nodes in a graph that defines the kind of relationship between the fundamental units (nodes). Here, a link between pair of nodes identify the movement between the two.
Connectivity	The minimum number of nodes whose removal disconnects the graph.
Area-weighted flux matrix	A measure of the probability of movement among pairs of nodes in a graph, based on specific characteristics of the nodes (e.g. surface, habitat availability).
Percolation point	The critical distance value for which the graph becomes disconnected.
Cluster	Set of nodes grouping together on the basis of common, shared properties as, for example, the similarity in terms of contribution to connectivity.
Random walk betweenness centrality	By definition, centrality refers to a set of measures that identify the most important nodes in a graph. Random walk betweenness is a measure of centrality based on counting how often a node is traversed by a random walk between two other nodes.
Centrality distribution	Is the distribution probability of centrality all over the graph. Different models give different interpretation about the robustness of the graph (see main text for further explanation).

the breeding, wintering and staging periods are key elements for the reproductive success and fitness of migrants (Both and Visser, 2001; Cotton, 2003).

Although past conservation strategies were mainly based on the maximization of biodiversity (Pressey et al., 1993), recent studies have shown the importance of connectivity in networks of protected areas (Mazaris et al., 2013; Bush et al., 2014; Magris et al., 2014). Specific aspects (e.g. spatial dynamics, dispersal pathways and migration strategies) should therefore be considered in the design of protected areas, to improve their ability to cope with changing climate conditions and ensure the long-term persistence of species (Mantyka-Pringle et al., 2012). The identification of how populations are geographically linked between different periods of the annual cycle is probably one of the biggest challenges in the conservation of migratory birds and the development of effective conservation strategies able to integrate year-round dynamics (Marra et al., 2006; Martin et al., 2007).

Despite its complexity, recent findings showed the feasibility of a flyway approach to model the connectivity among suitable areas for protecting migratory birds, improving the efficiency of resource allocation for the conservation of migrants (Iwamura et al., 2014). Modelling approaches to connectivity are often based on graph theory, where habitats and/or areas become part of a network of potentially interconnected nodes (Estrada and Bodin, 2008). Among many, node centrality and centrality distribution represent a set of measures able to quantify the degree of nodes importance (e.g. conservation areas) in relation to their ability to promote or impede the exchange of flow (e.g. birds movement) within the network (Estrada and Bodin, 2008). Moreover, their quantification allows obtaining information about the robustness of the system when subjected to different types of disturbances. Indeed, networks can show high robustness to random disturbances but not against targeted perturbations, which can have the potential to propagate faster through the network (Albert et al., 2000). Networks can also show critical transition points, where sudden collapses appear and the effects of targeted perturbations are likely to be very severe (Kéfi et al., 2011).

Such effects are of great importance in light of the localized impacts of climate change, which can influence in a non-random way the distribution and availability of suitable habitats, influencing the response of species in terms of migration rates and migratory behaviour (Erwin, 2009; Loarie et al., 2009). Latitude and elevation are, for instance, correlated with changes in temperature and precipitation, thus creating spatially structured patterns among regions. Such a spatial trend is found to be related with changes in the rate of precipitation, predicted to increase in the Asian monsoon region and decrease across the Mediterranean, South Africa and Australia (Pfahl et al., 2017). However, despite recent advances in spatial modelling techniques and reserve selection, a comprehensive framework linking migratory patterns and climate change at large spatial scale is still lacking.

In this work, I developed a methodological framework linking climate data with graph theory to test the ability of important conservation areas for migration to withstand the effects of changing climate conditions. To test this theoretical framework, I used data about the migratory activity of the northwestern European population of Eurasian spoonbills *Platalea leucorodia leucorodia*, undergoing a series of threats that result in a sharp decline in numbers and a restriction of their distribution. Given its high differentiated migratory behaviour (Lok et al., 2011), spoonbill represents a powerful study system to test how the influence of climate change on conservation areas may relate with different migration strategies. The increased mortality during long migrations is found to be driven by the presence of physical barriers (e.g. the Sahara desert), as well as by the suboptimal fuelling and unfavourable weather conditions *en route* (Lok et al., 2015), which make the preservation of this species priority within the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA).

Specifically, I wondered if the current spatial configuration of conservation areas is able to cope with changing habitat conditions, and how this relates with the spoonbill migration system (Lok et al., 2011). By keeping the approach an 'open framework', I show how to incorporate spatial and temporal dynamics into conservation planning, and compare the ability of conservation areas in sustaining the migratory activities of birds under climate change.

2. Materials and methods

2.1. General overview

A series of specific steps can be identified to model a network of conservation areas (see Table 1 for a summary of the most common terms used in this work) and predict their relative importance for migration in the face of changing climate conditions. Data about current and predicted climate can be used together with specific attributes of sites (e.g. surface area), as well as with their spatial attributes, to derive a measure of habitat availability to be integrated in the connectivity matrix (step 1, Fig. 1). In step 2 (Fig. 1), a measure of similarity is used to define the extent to which pairs of sites are equivalent in terms of contribution to the overall connectivity. Once obtained a pairwise similarity matrix, a patch connectivity criterion based on percolation theory (Stauffer and Aharony, 1992; Rozenfeld et al., 2008) is implemented to find the minimum connectivity network describing the pattern of species movement between sites (step 3, Fig. 1). Finally (step 4, Fig. 1), the relative importance of the sites for the overall connectivity is obtained by measuring their betweenness centrality.

2.2. Step 1: Measuring the potential connectivity

In this work, connectivity relies on a specific assessment of how the movement of individuals can be facilitated among conservation areas (i.e. functional connectivity), removing the potential biases associated

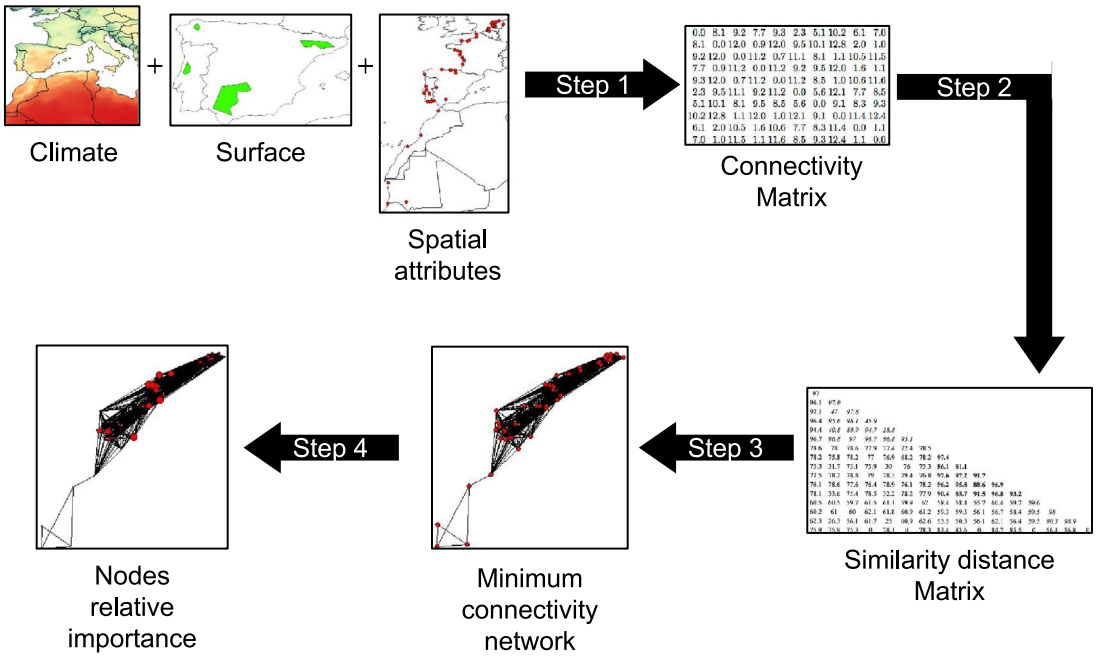

Fig. 1. Step diagram of the proposed framework, where each step describes a specific methodology involved in the derivation of: connectivity matrix (Step 1); similarity distance matrix (Step 2); minimum connectivity network (Step 3); nodes importance (Step 4).

with relying solely on the physical arrangement (e.g. geographic distance) of the landscape (Urban et al., 2009).

Here, connectivity was measured by using a modified version of the area-weighted flux (Bunn et al., 2000), by replacing the surface of areas with a surrogate measure able to quantify their contribution to the overall connectivity in terms of amount of available habitat. The habitat-weighted flux (*HWF*) can therefore be measured as:

$$HWF = \sum_{i=1}^{n} \sum_{j=1, i \neq j}^{n} p_{ij} H_i H_j \quad (1)$$

where n is the total number of sites and H_i and H_j the potential habitat availability of sites based on any relevant climatic feature (see Section 3.1). p_{ij} is the probability of species movement among pairs of sites, defined as:

$$p_{ij} = \exp(-\alpha d_{ij}) \quad (2)$$

where d_{ij} is the geographic distance between sites i and j and α a scaling parameter for the distance, able to incorporate different physiological capability of the species (e.g. the average site-to-site movement).

2.3. Step 2: estimate the pairwise similarity between sites

After measuring the degree of connectivity, patterns of relations among sites can be compared by a measure of similarity able to estimate the extent to which pairs of sites are functionally equivalent, that is, they have similar contribution in terms of number and weights of links to and from the other sites (Burt, 1988). In this work, sites in close proximity with similar values of H were considered more similar to distant sites differing in terms of habitat availability. Thus, similarity measures can help defining the extent to which sites diverge or not in their contribution to the overall network connectivity, where greater similarity equates to a greater probability of connectivity among sites.

Several distance metrics can be used to measure the degree of similarity between nodes in a network, having in mind that the correct evaluation is mainly a function of how relations are measured, rather than how similarities are measured (Burt, 1988). Some distance measures have the tendency to lose their sensitivity when data have asymmetric distributions, which can be the rule in spatial and ecological networks (Bode et al., 2008). To overcome this problem, the Sørensen similarity (also known as Bray-Curtis coefficient when applied to quantitative data, Faith et al., 1987) was used to measure the degree of similarity between pairs of sites, due to its higher performance when data are not normally distributed. Distance values were between 0 and 1, with values close to 0 indicating high similarity among sites and, therefore, high probability of connectivity.

2.4. Step 3: Finding the minimum connectivity network

The measured distance matrix (see above) depicts the probability of bird movement across a network of conservation sites, where not all sites have the same probability of connection. For instance, sites exceeding the dispersion probability of a species, as well as sites in close proximity but with low habitat availability should have less chance to be connected and, therefore, high values of dissimilarity. The identification of the spatial arrangement of sites and their connections is therefore fundamental for the correct evaluation of how individuals move through the network (Jacobson and Peres-Neto, 2010), and can be measured by identifying a distance threshold aimed at detecting which distance values should be depicted as links and which should not.

Among many, the use of percolation networks becomes increasingly used in ecological studies, allowing for the identification of the relationships among populations (Rozenfeld et al., 2008) or to identify critical scales in landscape ecology, having the advantage of not requesting any a priori knowledge of a threshold value. A percolation network arises when a critical threshold is reached, which is the minimum distance (the so-called percolation point) at which all sites are connected in a single network (Rozenfeld et al., 2008). The identification of this point is obtained by calculating the average cluster size, $\langle S \rangle^*$, (see Table 1), that is, the average number of sites belonging to an s-size cluster, as a function of the last threshold distance value beyond which links were removed (Stauffer and Aharony, 1992):

$$\langle S \rangle^* = \frac{1}{N} \sum_{s < S_{\max}} s^2 n_s \quad (3)$$

where N is the total number of sites not included in the largest cluster ($S_{\max}$) and n_s is the number of clusters containing s sites. Basically, each time a link (see Table 1) is removed from the network, sites are

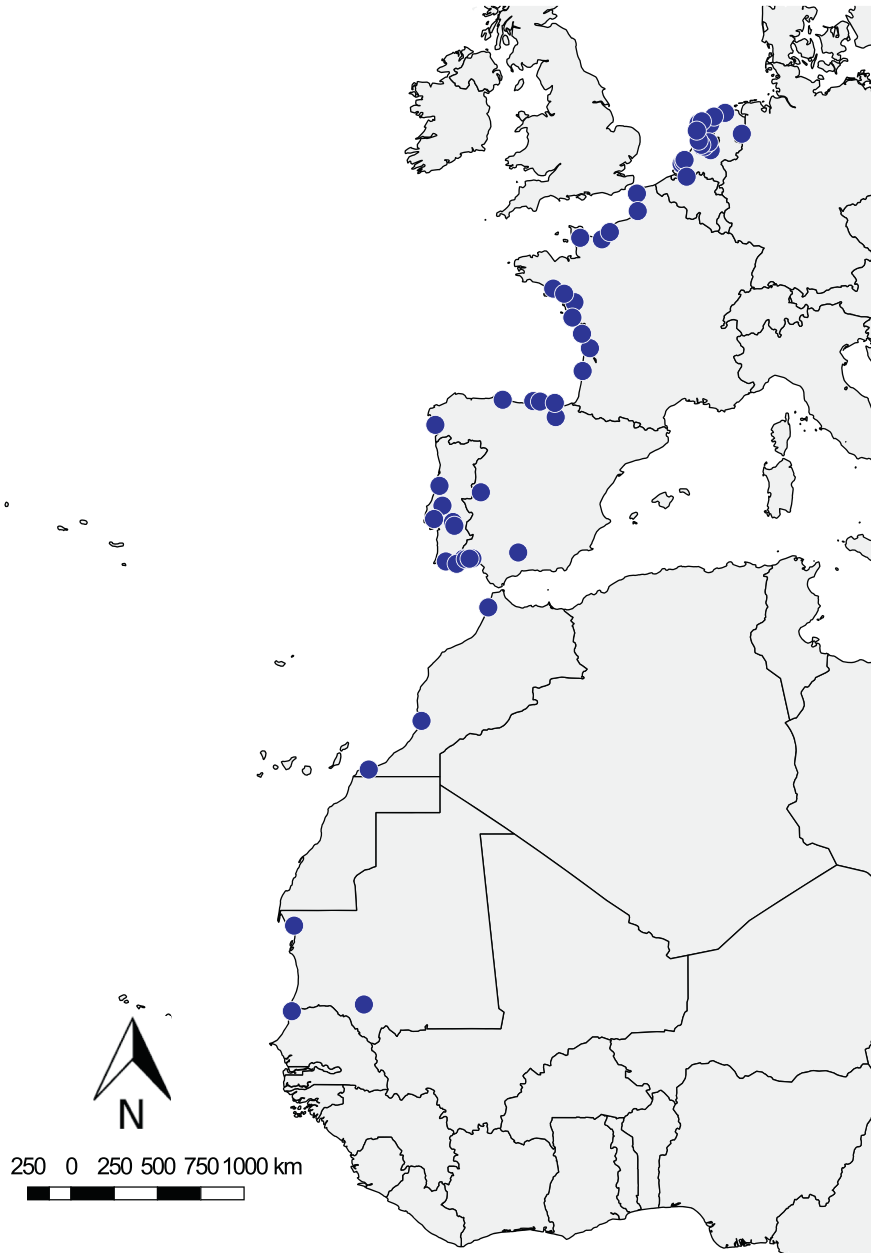

Fig. 2. Spatial distribution of selected conservation areas (blue points) for the Eurasian spoonbill, *Platalea leucorodia leucorodia* (http://datazone.birdlife.org/species/factsheet/eurasian-spoonbill-platalea-leucorodia/). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

redistributed in clusters of different sizes, from largest to smallest. This procedure is therefore iterated until a critical threshold is identified in the transitional region characterized by a strong decrease in $\langle S \rangle^*$, where the network become disconnected (for more information about percolation theory, refer to Stauffer and Aharony, 1992). Here, I used the methodology described in Rozenfeld et al. (2008) and implemented in the package 'sidier' of R (R Development Core Team, 2013).

2.5. Step 4: measuring the relative importance of sites

Different topological indexes have been extensively used in the past to measure the positional importance of the nodes within different types of networks. Centrality encloses a wide range of measures able to identify the role of a node with respect to its neighbours or the entire network (Estrada and Bodin, 2008). Among many, betweenness centrality considers the number of shortest paths from all nodes to all others that pass through that node, and can be considered a measure of the influence a node has over the movement of individuals throughout the network. Although many species migrate along broadly similar routes (e.g. the flyways), weather patterns, *en route* resources and geographical features (e.g. coastlines, mountains or wide offshore areas) mean that birds not necessarily take the shortest route (Berthold, 2001). Therefore, excluding all the possible routes among sites in a network may underestimate the potential role of those not included in the shortest paths.

A measure of betweenness based on random walks (hereafter β_{rw}) was thus used to measure the positional importance of sites in the network. This measure counts all the paths between sites (i.e. how often a site fall on a random walk between another pair of sites), making no assumptions of optimality (Newman, 2005). Strictly speaking, sites with high β_{rw} are likely to be crucial in providing traversability for species movement, because reduce the overall network distance bringing together isolated sites and/or groups of sites (Bodin and Norberg, 2006). β_{rw} was measured by means of the Network Prioritizer Tool (Kacprowski et al., 2013), available as a plug in for Cytoscape (Shannon et al., 2003).

The distribution of centrality within the network can be tested by fitting the cumulative distribution of β_{rw} to different models. Model

fitting allows measuring the degree of asymmetry/symmetry in the distribution of centrality, or to find critical values of centrality over which the distribution exhibits patterns that might indicate a sudden collapse of the system. A power law model, $P(\beta_{rw}) \sim \beta_{rw}^{-\gamma}$, typically describes asymmetry in the cumulative distribution of centrality, where the bulk of sites have low values of β_{rw} and only few sites high β_{rw}. Conversely, a more homogeneous distribution is given by an exponential model, $P(\beta_{rw}) \sim \exp(-\gamma\beta_{rw})$, while a truncated power law (i.e. a power law with exponential cut-off), $P(\beta_{rw}) \sim \beta_{rw}^{-\gamma} \exp(-\beta_{rw}/\beta_{rw[x]})$, typically exhibits a faster exponential decay at some critical level (i.e. the cut-off point, $\beta_{rw[x]}$). Different distribution models imply different degree of robustness, defined as the ability of a network to withstand perturbations, simply because the probability of removing sites with high centrality differs among networks.

Fitting models were compared by using the Akaike's information criterion (AIC, Burnham and Anderson, 1998), and best models were expressed by AIC differences, ΔAIC = AIC − min(AIC) and Akaike model weights.

3. Application of the framework, a case study: the Eurasian spoonbill *Platalea leucorodia leucorodia*

Effects of changing climate conditions were evaluated on the potential connectivity of conservation areas for the northwestern population of Eurasian spoonbills *Platalea leucorodia leucorodia,* which breed in The Netherlands and winter along the East-Atlantic coast between France and Senegal. The Eurasian spoonbill is classified as being of 'Least Concern' in the 2006 IUCN Red List of Threatened Species, and all populations fall within the International Single Species Action Plans (ISSAPs) under the AEWA agreement. AEWA is an intergovernmental treaty dedicated to the conservation of migratory waterbirds and their habitats, bringing together regions as Africa, Europe, the Middle East, Central Asia, Greenland and the Canadian Archipelago with the aim of implementing a set of coordinated activities for the conservation and management of migratory waterbirds throughout their entire migratory range. The northern populations of Eurasian spoonbills are comprised between 10,000 and 25,000 individuals and show an interesting migratory behaviour, with most birds travel to where survival rates are lowest, in what some authors called 'the paradox of spoonbill migration' (Lok et al., 2011, 2015).

Here, conservation areas including the breeding sites in The Netherlands and wintering sites along the East-Atlantic coast between France and Senegal (http://datazone.birdlife.org/species/factsheet/eurasian-spoonbill-platalea-leucorodia/) were used to model the potential network of conservation areas (Fig. 2). Steps 1 to 4 were iterated for current and projected climate conditions on the southward migration system of spoonbills, to test if: i) conservation areas differ in their contribution to the potential movement of birds, ii) current and projected networks differ in terms of robustness and, iii) conservation areas are able to support the spoonbill migration system in the face of changing climate conditions.

3.1. Quantifying habitat quality and availability

As many other migratory birds, the Eurasian spoonbill largely depends on wetlands, which provide migrants with appropriate cover in which to rest, refuel, and seek protection from predators and inclement weather before moving. Moreover, the state of wetlands in the breeding area may also have a significant influence on the decision to whether or not start to breed. Therefore, providing an adequate estimate of the amount of available habitat for sustaining the migratory activity is essential to model the potential movement between sites.

First, a surrogate measure of habitat quality was quantified by means of the Aridity Index (*AI*), a dimensionless index which expresses the precipitation availability over atmospheric water demand, and represents a numeric quantification of the balance between rainfall and evapotranspiration. *AI* was measured as $AI = P_\mu/PET_\mu$, with P_μ and PET_μ the mean monthly precipitation and potential evapotranspiration, respectively, averaged over the reference period corresponding to the end of summer (July–September) in the breeding areas of Palearctic zone (Lok et al., 2015). *AI* values were then normalized in a 0–1 scale as $AI^* = [AI - \min(AI)]/[\max(AI) - \min(AI)]$, with values close to 0 indicating extreme dry conditions ($PET_\mu \gg P_\mu$) and values close to 1 extreme wet conditions ($PET_\mu \ll P_\mu$). *AI* can be used as a proxy for potential wetlands distribution, whose changes in water deficit may influence the ability of wetland-dependent species to move between patches of suitable habitats (McIntyre et al., 2014). The potential evapotranspiration was measured following the general Hargreaves method (Hargreaves et al., 1985), applied to each monthly climate data (see after):

$$PET = 0.0023 \cdot RA \cdot (T_{mean} + 17.8) \cdot T_D^{0.5} \quad (4)$$

with T_{mean} and T_D the mean monthly temperature and mean monthly temperature range, respectively and *RA* the extraterrestrial radiation (i.e. radiation on top of atmosphere) measured following Allen et al. (1998):

$$RA = \frac{24(60)}{\pi} G_{sc} d_r [\omega_s \sin(\varphi) \sin(\delta) + \cos(\varphi) \sin(\delta) \sin(\omega_s)] \quad (5)$$

where G_{sc} is the solar constant, d_r the inverse relative distance between earth and sun, ω_s the sunset hour angle, φ is the latitude and δ the solar decimation value (for further details about the formula, refer to Allen et al., 1998). Despite the relative simplicity of the Hargreaves method, some authors pinpointed on its ability to measure *PET* at large (global) scale, requiring less parametrization than more complex models and therefore reducing the sensitivity to error in climatic inputs (Hargreaves and Allen, 2003).

Finally, a surrogate measure of the available habitat for each conservation area, H_i, can be derived by multiplying its surface (log-transformed to improve normality) by a 'penalty' values given by AI^*. Therefore, for $AI^* \sim 1$ (i.e. extreme wet conditions) the amount of suitable habitat will be approximately equal to the surface of the area.

3.2. Climate data

The *AI* index was measured by considering the migration system of spoonbill moving to the breeding sites located in The Netherlands and Germany and moving southward to the wintering sites between France and Senegal. *P*, *T* and T_D were downloaded as bioclimatic variables from the WorldClim dataset (http://www.worldclim.org/bioclim) (Hijmans et al., 2005). A multi-model ensemble mean of 14 GCMs from CMIP5 (Coupled Model Intercomparison Project Phase 5, http://cmip-pcmdi.llnl.gov/cmip5/) was used to analyse precipitation, mean, minimum and maximum temperature. Data were downloaded as downscaled CMIP5 layers at 30 arc *sec* (~900 m at equator) for the most critical greenhouse gas concentration trajectories (Representative Concentration Pathways, RCPs). In this work, I referred only to projections that were forced with the high end emission scenario RCP8.5, which reflect the increasing rise of greenhouse gas emissions through the 21st century. Climate data were derived for the current (1950–2000) and late-21st century (2061–2080) conditions. Differences in AI^* among climate scenarios were measured by $\Delta AI^* = AI^*_{\text{curr}} - AI^*_{\text{prj}}$, with values of $\Delta AI^* > 0$ and $\Delta AI^* < 0$ indicating a decreasing and increasing AI^* in the future, respectively.

Although, the use of a limited number of scenarios is by no mean sufficient to disentangle all the uncertainties related with changing climate conditions, the high end emission scenario was used to keep the approach as conservative as possible with respect to the ability of conservation areas to provide functional connectivity in the future. However, the theoretical framework is open to incorporate as much information as possible, including further projections to compare different planning scenarios.

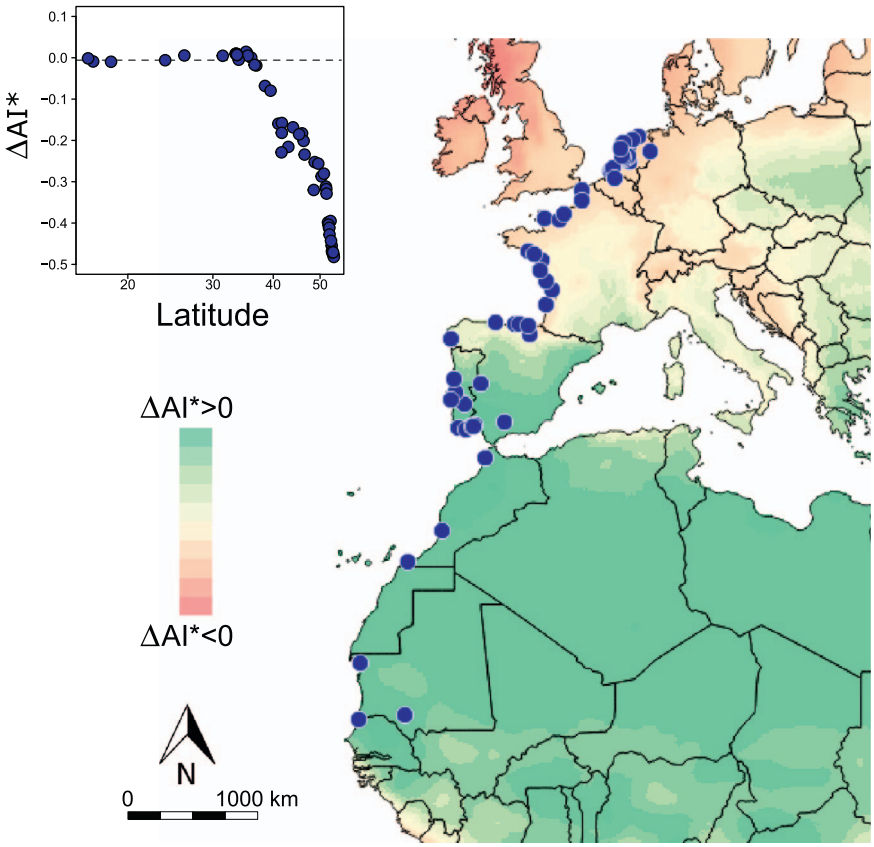

Fig. 3. Map of the geographic distribution of the aridity index differences ($\Delta AI^* = AI^*_{curr} - AI^*_{prj}$) between climate scenarios. $\Delta AI^* > 0$ and $\Delta AI^* < 0$ indicate the decrease and increase of aridity conditions, respectively. Graph on the top left shows the latitudinal distribution of ΔAI^*.

3.3. Integrating average site-to-site distance to measure the probability of spoonbill movement across areas

The last parameter needed for modelling the potential movement of spoonbill across the network of conservation areas is given by the term $\alpha = 1/r$ in Eq. (2), with r the average site-to-site distance. The precise identification of r in the Eurasian spoonbill (as many other migrants) is not easy to derive, as the northwestern populations are characterized by different migration systems, with individuals able to cover distance between 1000 up to 4000 km (Lok et al., 2015). Spoonbills developed different stopover strategies depending on the expected distance of migration, with long-distance migrants able to by-pass specific stopover area to reduce the potential effects of density-dependent process during migration (Lok et al., 2011, 2015). Migratory strategies are extremely variable, with some populations covering small steps (around 100–300 km) and rest for a few days at stopover sites, while others make large steps (1000–2000 km) and stop for longer periods to recover (Lok et al., 2011). Here, values of $r = 300$ km and $r = 2000$ km were used in Eq. (2) as the average site-to-site distance, indicating the short- and long-distance migration strategies of the Eurasian spoonbill, respectively.

Sensitive areas for migration was measured starting from the positional deviance in the rank of sites based on β_{rw}:

$$\Delta\beta_{rw} = {}^{rk}_{curr}\beta - {}^{rk}_{prj}\beta_{rw} \quad (6)$$

where rk indicates the rank of a site based on its value of β_{rw} under the current and projected climate scenario. Values of $\Delta\beta_{rw} > 0$ and $\Delta\beta_{rw} < 0$ indicate a decrease or increase in the ranking of sites, respectively. Sites with $\Delta\beta_{rw} = 0$ are expected to not deviate their positional importance. The non-parametric Mann-Whitney U test was used to test for differences in the values of β_{rw} among migration strategies and climate scenarios.

4. Results

4.1. Spatial effects of climate change on AI

The multi-model ensemble mean of the selected 14 GCMs showed differences in the spatial distribution of AI among the Palearctic region and the Afrotropic ecozone (Fig. 3). This latter was characterized by a predicted (even small) decrease of AI ($\Delta AI^* > 0$), with a relatively narrow area located immediately below the Sub-Saharan zone with $\Delta AI^* < 0$, indicating an increase of aridity conditions in the future. In the Palearctic region, the increase of AI was much more pronounced, observing a greater portion of territory subjected to this phenomenon with increasing latitude (Fig. 3). Sites showed an interesting spatial pattern, with an abrupt change in the distribution of ΔAI^* at around 40° latitude, where all sits were characterized by $\Delta AI^* < 0$ (Fig. 3).

4.2. Network analysis

4.2.1. Minimum connectivity network

When considering the short-distance migration strategy, the percolation analysis revealed a functional threshold of 0.86 for current climate conditions, and 0.82 for future projections. As a consequence, the network of conservation areas for the Eurasian spoonbill was composed of $n = 53$ sites with $L_{current} = 809$ and $L_{prj} = 740$ links. For long-distance migrants, the thresholds under the current and projected climate scenario were 0.46 and 0.21, respectively, with $L_{current} = 792$ and $L_{prj} = 647$ links.

4.2.2. Importance of conservation areas

Nodes centrality showed significant differences between climate scenarios (Mann-Whitney U test, $U \approx 1000$ and $p \approx 0.01$ in both cases) and migration strategies (Mann-Whitney U test, $U < 300$ and $p < 0.001$ in both cases). However, when considering short-migration

Table 2
Model fitting of the random-walk betweenness centrality (β_{rw}) under current and projected climate scenarios for the Eurasian spoonbill conservation areas. Bold indicates the best model for each network: Exp, exponential; Pow, power law; Tru, truncated power law (i.e. power law with exponential cut-off). *r*, the average site-to-site migration distance (km); d.f. are the degrees of freedom; γ the scaling exponent ($\gamma > 0$); $\beta_{rw[x]}$ the threshold value of centrality for a truncated power law distribution (i.e. the value beyond which the distribution change from a power to an exponential law); ΔAIC = AIC - min(AIC); AICw the Akaike Model Weights.

Scenario	*r*	Model	d.f.	γ	$\beta_{rw[x]}$	AIC	ΔAIC	AICw
Current	300	**Exp**	2	2.945		− 205.584	0	$3.93(10^{-24})$
		Pow	3	0.215		− 98.324	107.26	$2.01(10^{-47})$
		Tru-Pow	3	0.013	0.347	− 202.761	2.823	$9.59(10^{-25})$
	2000	Exp	2	1.882		− 247.857	25.433	$5.949(10^{-15})$
		Pow	3	0.267		− 143.963	129.327	$1.637(10^{-37})$
		Tru-Pow	3	0.039	0.506	− 273.29	0	$1.982(10^{-9})$
RCP8.5	300	Exp	2	2.453		− 201.306	10.572	$4.635(10^{-25})$
		Pow	3	0.208		− 131.801	80.077	$3.743(10^{-40})$
		Tru-Pow	3	0.022	0.396	− 211.878	0	$9.156(10^{-23})$
	2000	Exp	2	2.722		− 312.374	0	$6.083(10^{-1})$
		Pow	3	0.199		− 199.174	115.2	$1.59(10^{-25})$
		Tru-Pow	3	0.002	0.366	− 311.493	0.881	$3.916(10^{-1})$

strategies (average site-to-site distance, $r = 300$ km), the distribution of betweenness centrality for current *AI* conditions showed a uniform distribution, as indicated by the exponential cumulative distribution of β_{rw} (Table 2 and Fig. 4). Conversely, a less uniform distribution has been observed for the projected *AI*, where the cumulative distribution of β_{rw} showed a truncated power law (i.e. a power law with exponential cut-off, Table 2 and Fig. 4), suggesting the existence of a threshold beyond which the network might show a sudden collapse. For the long-distance migration strategy (average site-to-site distance, $r = 2000$ km), centrality is expected to have a truncated power-law distribution for the current *AI*, while no single model was able to explain the distribution of centrality under projected conditions, with centrality falling within a truncated power-law and an exponential model (Table 2 and Fig. 4).

Differences in the rank of β_{rw} were quite similar for both migration strategies, observing how about 15% of sites have been characterized by a $\Delta\beta_{rw} = 0$, that is, their rank did not change between current and projected climate. About half of the sites were expected to increase their centrality ($\Delta\beta_{rw} < 0$), while 30–38% should decrease their positional importance within the network. The distribution of such changes had also an interesting spatial patterns, with a core of sites located within the Iberian peninsula and The Netherlands showing the same change regardless of migration strategies (Fig. 4A and B). Major changes can be observed for sites expected to maintain their positional importance. For short-distance migrants these sites are distributed throughout the network, with 1 site in the breeding areas of The Netherlands, 2 in the stop-over/wintering areas of the Iberian peninsula and 3 between Morocco and Mauritania (Fig. 4A). When considering the long-distance migration system, it can be observed a gap between central France (2 sites) and Mauritania (3 sites), with no sites of $\Delta\beta_{rw} = 0$ in the central part of the network (Fig. 4B).

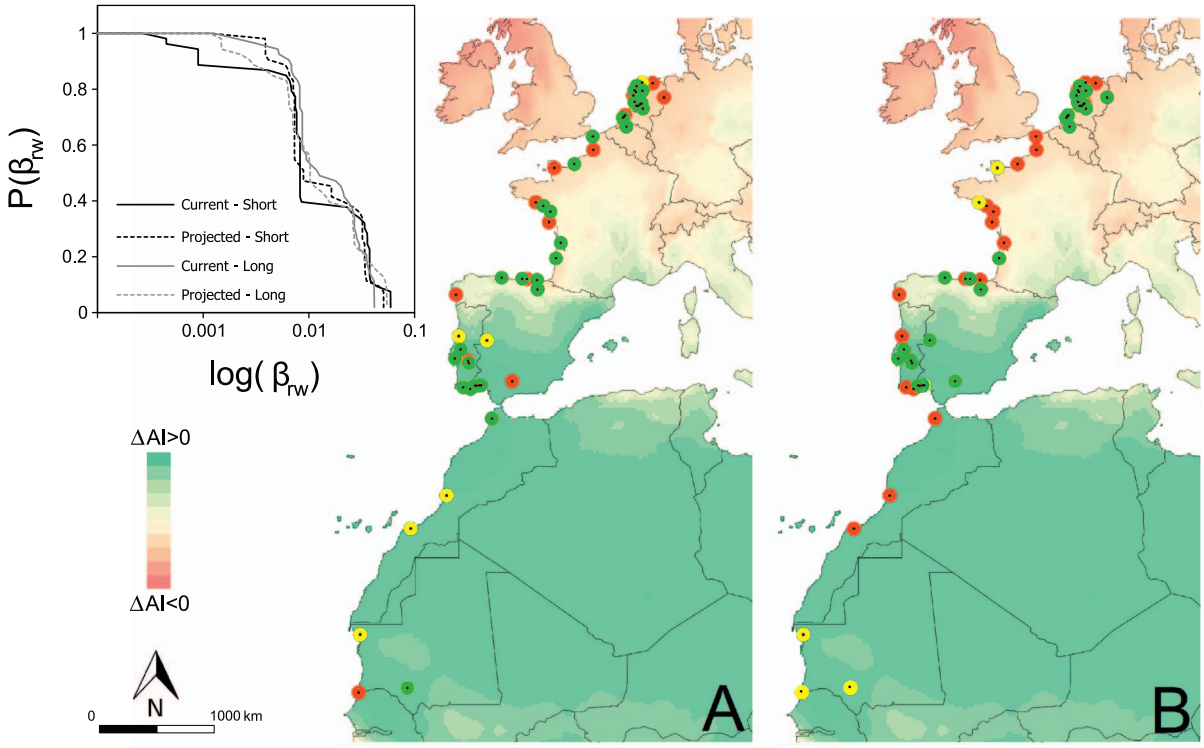

Fig. 4. Map showing the distribution in the differences of centrality rank among climate scenarios ($\Delta\beta_{rw}$) for: A, short-distance migrants (average site-to-site movement, $r = 300$ km) and B, long-distance migrants ($r = 2000$ km). Red nodes are for sites expected to decrease their positional importance ($\Delta\beta_{rw} > 0$), green for sites with increasing positional importance ($\Delta\beta_{rw} < 0$) and yellow for nodes having the same positional rank ($\Delta\beta_{rw} = 0$). Graph on the top left shows the cumulative distribution of betweenness centrality for short- and long-distance migrants under different climate scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Discussion

In this work, the migratory system of the northwestern populations of Eurasian spoonbill is found to be strongly influenced by the impacts of changing climate conditions on the network of conservation areas. Spoonbills having short-migration strategies could be less impacted by changing aridity conditions, while those populations having far long migratory activities might face major issues. Climate is found to contribute to changes in the quality and (possibly) quantity of suitable habitats, increasing fragmentation and diminishing the potential connectivity of the network. As a consequence, connectivity is conserved for neighbouring areas, while distant ones become more and more isolated, increasing the cost associated with migration. This can represent a major concern for individuals wintering in the Afrotropic zone (i.e. Mauritania and Senegal), as spoonbills show an age-dependent fidelity in wintering sites, with adults migrating southwards between their first and second winter and stay faithful afterwards (Lok et al., 2011). The same can be applied for individuals wintering in European regions, although they have a significantly lower site fidelity, possibly indicating more plastic responses to sub-optimal migration conditions.

Overall, the exponential and truncated power-law were the two models describing the cumulative distribution of centrality within the network. Under current climate and for short-distance migrants, the network is robust enough to counteract the loss of suitable habitats due to targeted or random impacts. This is because in the exponential distribution sites have quite similar values of centrality, so that the probability of losing high-connected sites is very low. Conversely, the truncated power-law distribution for long-distance migrants show a critical value of centrality beyond which the distribution exhibits a sudden collapse, and were the effects of targeted perturbations are likely to be more severe. This is because, in systems with a truncated power-law distribution, few sites act as hubs able to maintain the cohesion of entire network. Therefore, localized perturbations able to destroy such sites have the ability to propagate faster and undermine the overall network cohesion. Such results are of great importance in light of the localized effects of climate change, which can impact in a non-random way the distribution and availability of suitable habitats for migratory birds.

Although a general consensus about the spatial impact of climate change is far from being achieved (e.g. the wet-gets-wetter, Held and Soden, 2006, and the warmer-gets-wetter hypothesis, Xie et al., 2010), climatic differences among distant areas should increase on a large spatial scale (Pfahl et al., 2017). This may be due to the uneven and localized impact of changing climate conditions, which have found to follow well-defined geographic and regional patterns (Erwin, 2009; Loarie et al., 2009). The spatial distribution of the potential climate effects on *AI* has shown a separation between the Palearctic region and the Afrotropic ecozone, with this latter characterized by a general positive trend in the variation of *AI*. In the Afrotropic, *AI* is predicted to increase along a large and confined area located just below the Sub-Saharan zone, while in the Palearctic region the effects of changing climate on *AI* are expected to be much more pronounced. This can increase the risk of population declines because of a contraction of suitable habitats in key areas during migration (Jonzén et al., 2006; Charmantier and Gienapp, 2014).

For both migration strategies, the bulk of sites is expected to increase their relative importance for the cohesion of the network, the majority of which located in the breeding areas of the Netherlands and in the stop-over/wintering areas of the Iberian peninsula. Sites expected to decrease their importance are instead located along a more homogeneous route, spanning from the breeding sites in the Palearctic region until the wintering sites located in the Afrotropic ecozone. Conservation areas with zero deviance, that is, areas that did not change their position between climate scenario regardless their contribution to the overall network cohesion, had a different geographic distribution when considering migration strategies. For short-distance migrants, these sites are mainly localized between south of the Iberian peninsula and Morocco and Mauritania, while for long-distance migrants they are localized in the northernmost part of the Palearctic zone and in the southernmost one of the Afrotropic ecozone.

Such a geographic subdivision is even more important because of the peculiarity of the Eurasian spoonbill migration system, which is characterized by most birds migrating southward from the breeding sites located in the Netherlands to the southernmost wintering region (Mauritania and Senegal) to where survival rates are lower (Lok et al., 2011). Although the causes of such behaviour are still not clear, the results obtained in this work reinforce the view that the slow evolutionary responses of spoonbill can magnify the threat of changes to its migratory network (Lok et al., 2011). Differences in the relative importance of conservation areas over large spatial extent could amplify the mismatch in timing of migration because long-distance migrants may be limited in their responses to changing conditions at sites due to the greater distances to cover or to their stronger endogenous control of migration timing (Cotton, 2003).

Generally, bird migrating from Palearctic to Afrotropic Regions have to compete with other migrants and residents, even in times with lowest resource abundance within the annual cycle (Moreau, 1972; Salewski et al., 2003). Besides the availability of food resources in the winter quarters, the distribution of many Palearctic migrants also depends on the climate effects in wintering areas, as changes in rainfall regimes (Evans et al., 2012). Therefore, whether or not the mechanisms behind the responses are the results of individual plasticity in timing of migration, true microevolutionary responses or environmentally-induced plastic responses (Pulido and Berthold, 2004; Gienapp et al., 2008), the current spatial configuration of the network unlikely will be helpful for long-distance migrants.

In this work, a series of useful information for modelling the network of conservation areas have been omitted. Indeed, data about population dynamics, species dependencies, plasticity in migratory behaviours, as well as habitat configuration occurring outside the protected areas could enhance the predictive ability of the model and, therefore, should be used when available. For example, a measure of changes in water depth between climate scenarios could increase the predictive ability of the model, in view of the foraging ecology of spoonbill that largely depends on the presence of wetlands with suitable water depth (Pigniczki and Végvári, 2015). Leaving the proposed methodology an open framework, this can be applied to other migratory systems, having as only limit the use of spatially explicit data. Indeed, different ecological information can be used to test specific hypotheses, by using the most appropriate measures relating the ecology of studied species with different characteristics of habitats as, for example, the amount of available hardwood forest during stopover in terrestrial birds (Buler and Moore, 2011).

6. Conclusions

Effects of climate change on the migratory activity of Eurasian spoonbill can be amplified by the geographic configuration of existing conservation areas, with deleterious effects on bird populations, especially long-distance migrants. The observed displacement between Palearctic and Afrotropic sites would suggest greater distance to cover for long-distance migrants, increasing the risk of fragmentation and contraction of populations, unlikely to support the spoonbill migration system. How the evolutionary responses of spoonbill relate with the observed changes in the network of conservation areas still remains a major objective for the protection of the species.

This reinforce the view that the actual conservation policies could not be sufficient without the identification of the functional pathways able to guarantee the movement of species. Such aspect is also critical for the effective adaptation of migrants to climate change and their ability to increase their dispersal into new regions. From a practical point of view, these results are of great importance, as they are linked

with the identification of conservation priorities. Changes (whether positive or negative) in the role played by conservation areas differ widely in what may be the potential migration routes. If the ultimate goal of conservation is the maintenance of migration flows, the priority should be given to areas having consistently high betweenness over time, which should be considered real 'hot-spots' as they represent key areas able to guarantee a certain stability in the movement pathway. Therefore, alongside predictive models of species distribution, future conservation approaches should take in account the role of conservation areas in maintaining the functional connectivity of migrants between different periods of the annual cycle (Marra et al., 2006; Martin et al., 2007).

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